ELSEVIER

Forest Ecology and Management 129 (2000) 177–193

Forest Ecology and Management

www.elsevier.com/locate/foreco

Regenerating uneven-aged stands of loblolly and shortleaf pines: the current state of knowledge

Michael G. Shelton*, Michael D. Cain

USDA Forest Service, Southern Research Station, Monticello, AR 71656-3516, USA

Received 30 October 1998; accepted 6 May 1999

Abstract

Periodic regeneration is crucial to creating or sustaining uneven-aged (UEA) stands of loblolly (*Pinus taeda* L.) and shortleaf (*P. echinata* Mill.) pines. Although both species are shade intolerant, they have silvical characteristics that are conducive to natural regeneration in UEA stands. Their seed production is fairly consistent and good, and the wind-disseminated seeds are well dispersed throughout the stand. The disturbed seedbed resulting from periodic logging is favorable to germination, and established seedlings can recover from a fair degree of logging damage. Seedlings are moderately shade tolerant when young, and they respond well when released from either competing understory vegetation or overtopping trees. The key to successful regeneration in UEA pine stands involves regulating the stocking and structure of the merchantable portion of the stand with careful logging and periodically controlling nonpine vegetation, typically with selective broadcast herbicides[1]. Current after-cut guidelines call for basal areas of 10 to 14 m^2/ha, maximum diameters of 35 to 55 cm, and a *q* factor in the vicinity of 1.2 for 2.5 cm DBH classes. Applying these guidelines results in a stand with an irregular canopy containing multidimensional gaps. Stand basal area is not allowed to exceed 17 m^2/ha during the cutting cycle because regeneration would be adversely affected by shading and root competition. Pines over 40 cm in DBH have been found to be favorable to regeneration because of increased seed production and reduced logging traffic needed to remove harvested trees. Regeneration is most difficult to secure on good sites because of intensive nonpine competition, but selective herbicides are available that will release pine regeneration from competing nonpine vegetation. Due to the increased interest in UEA silviculture, we present an overview in this paper of more than 50 years of research and experience in regenerating these two important species in UEA stands principally using single-tree selection.

Keywords: Competing vegetation; Natural regeneration; *Pinus taeda*; *Pinus echinata*; Seed production; Seedbed conditions; Single-tree selection

1. Introduction

Loblolly (*Pinus taeda* L.) and shortleaf (*P. echinata* Mill.) pines are common associates throughout most of the southeastern United States and are among the most important and widespread of the southern pines (Baker and Langdon, 1990;

*Corresponding author: Tel.: +1-870-367-3464; fax: +1-870-367-1164.
E-mail address: mshelton/srs_monticello@fs.fed.us (M.G. Shelton).

[1]This publication reports research involving herbicides. It does not contain recommendations for their use, nor does it imply that the uses discussed here have been registered. All uses of herbicides must be registered by appropriate state and/or federal agencies before they can be recommended.

0378-1127/00/$ – see front matter
PII: S0378-1127(99)00161-9

Lawson, 1990). These two species share many silvical characteristics. Both can be regenerated naturally using either even-aged or uneven-aged (UEA) techniques. While UEA silviculture has classically been applied to species that can regenerate and develop in partial shade (Marquis, 1976), it has also been successfully applied to some of the shade-intolerant southern pines, principally loblolly and shortleaf pines (Murphy et al., 1991; Baker et al., 1996; Farrar, 1996; Guldin and Baker, 1998) and to a limited extent longleaf pine (*P. palustris* Mill.) (Farrar and Boyer, 1991). This success depends on regulating the stocking and structure of the merchantable trees in the stand through periodic harvests and controlling the speciescomposition of the understory and mid-canopy, chiefly with broadcast application of selective herbicides. Such practices yield high rates of merchantable growth and create a favorable environment for the establishment and development of pine regeneration (Reynolds, 1959; Williston, 1978; Baker et al., 1996).

Periodic regeneration is crucial in creating or sustaining UEA stands. The goal of any reproduction cutting method is to provide a favorable environment for establishment and development of the desired species. As with most forestry operations, obtaining successful natural regeneration in UEA stands bears certain risks. However, these risks can be minimized by understanding the factors affecting the regeneration processes and applying appropriate silvicultural practices. Numerous factors interact to determine the success of natural regeneration. Seed production and seedbed conditions affect the initial establishment of regeneration, while competition from merchantable trees and understory vegetation affect subsequent development by determining the amount of light, water, and nutrients available to desired regeneration. Knowledge of these factors and processes serves as a scientific basis for adapting UEA silviculture to a wide range of stand and site conditions. Although much has been published on regenerating UEA stands of loblolly and shortleaf pines over the last 50 years, there is a need to document these basic tenets in a single source because of the increased interest in UEA silviculture (Guldin and Baker, 1998; O'Hara, 1998).

2. Factors affecting natural regeneration

2.1. Merchantable trees (DBH > 9 cm)

2.1.1. Competition effects

Loblolly and shortleaf pines require abundant light for rapid growth, and regeneration grows best under full sunlight (Mattoon, 1915; Wahlenberg, 1960; Schultz, 1997). Due to their intolerance to shade in the second or third year after establishment, growth of pine seedlings will be somewhat suppressed under any regeneration method that retains an overstory (Chapman, 1945; Wahlenberg, 1948; Jackson, 1959; Ferguson, 1963). Thus, for successful UEA silviculture of loblolly and shortleaf pines, there must be a compromise between retaining adequate overstory stocking for acceptable merchantable growth and reducing the overstory to provide acceptable environmental conditions for regeneration.

Both loblolly and shortleaf pine seedlings can become established under a dense canopy and persist for several years before dying (Becton, 1936; Wahlenberg, 1960). This observation suggests that newly established pine seedlings are moderately shade tolerant but become more shade intolerant with age. Bormann (1956) reported, for example, that the photosynthetic efficiency of loblolly pine seedlings at low light intensities declined substantially as secondary foliage developed.

When recommended guidelines for single-tree selection are applied, a pine stand with an irregular canopy and many gaps of various sizes results. Irregularly shaped openings of up to 0.1 ha can occur with virtually no merchantable trees, and these merge into clumps and clusters of trees with a closed canopy. Multiple occupancy is common both for merchantable trees and for regeneration. Although regeneration becomes established throughout stands under single-tree selection, we are most concerned with establishment and development of regeneration in gaps created by harvesting merchantable trees. Observation indicates that some regeneration becomes established after gaps are formed but other seedlings and saplings may exist before gap formation.

Light intensity beneath an UEA pine canopy is highly variable spatially, ranging from near full sunlight to a partial light regime where sunflecks occur periodically. The stocking of merchantable trees strongly affects the mean light intensity near ground level in pine stands (Guo and Shelton, 1998). The Guo and Shelton model predicts that loblolly-shortleaf pine stands with basal areas of 10 to 17 m^2/ha, the recommended stocking limits for UEA stands, have light intensities of 73% to 50% of full sunlight, respectively, when the sun is close to its daily zenith during summer. The sparse canopy in UEA pine stands is also indicated by a relatively low percentage of canopy coverage, which averaged 55% in a shortleaf pine stand with basal area of 13.5 m^2/ha (Shelton and Murphy, 1997). We feel that maximum diameter used in stand regulation will also affect the degree and type of shade produced by the canopy, but this has yet to be confirmed by research. This relationship seems logical because taller trees are retained in stands with the higher maximum diameters. Height of the canopy in even-aged stands has been shown to affect the rate of height growth of loblolly pine seedlings – a high canopy resulted in less suppression than a low canopy because of differences in shade levels (Brender and Barber, 1956).

In intensively managed UEA pine stands, hardwoods are usually not allowed to develop into mid-canopy positions because their deep shade adversely affects the growth of merchantable pines and the establishment and growth of submerchantable pines. Guo and Shelton (1998) showed that hardwoods produce about twice the amount of shade as the same basal area in loblolly and shortleaf pines. They attributed this difference to the broad leaves, robust crowns, and shorter heights of hardwoods when compared to the pines. Thus, a scattered distribution of many merchantable-sized hardwoods (perhaps over 1 or 2 m^2/ha in basal area) is not silviculturally possible in pine stands being managed by single-tree selection. However, landowners wanting to enhance nontimber resources can retain hardwoods along drainages or in clusters outside areas designated for pine timber production. Group selection may also permit substantial hardwood retention in the residual stand because the larger openings provide the higher light intensities needed for development of shade-intolerant species (Shelton, 1998).

2.1.2. Regulation

Proper regulation of stocking and structure of merchantable trees is a critical element of successful regeneration. Detailed guidelines for regulating UEA stands of loblolly and shortleaf have been published (Baker et al., 1996; Farrar, 1996), and only a brief description will be given here to provide continuity to our discussion of regeneration processes. Several regulation techniques have been successfully applied in UEA stands of loblolly and shortleaf pines. In this paper, we have focused on application of the basal area–maximum diameter–q method, which is an objective regulation method frequently used in research studies. Maximum diameter (the largest tree in the residual stand) and the q factor (ratio of the number of trees in successive DBH classes) are varied in this method to control the shape of the diameter distribution in the residual stand. Current after-cut guidelines call for merchantable basal areas of 10 to 14 m^2/ha, maximum diameters of 35 to 55 cm, and a q factor in the vicinity of 1.2 for 2.5 cm DBH classes. The q factor is the least important of the variables and the most difficult to control in UEA stands of loblolly and shortleaf pines. Most operational-level UEA pine stands will consist of multiple age or size classes, rather than adhering to a classic balanced reversed-J distribution representing an all-aged structure. In applying UEA regulation methods, a tree's size, quality, and ability to respond to release are of more importance than its age. For example, Baker and Shelton (1998) reported that suppressed pines that were 45 years old and 13 cm in DBH grew to 32 cm within 15 years of release in UEA pine stands.

Stocking in merchantable-sized trees in UEA pine stands is maintained at less than full occupancy so that some of the site's resources (light, water, and nutrients) are available to regeneration. Merchantable basal area is never allowed to exceed 17 m^2/ha during the cutting cycle because the development of pine regeneration is adversely affected by shading and root competition from overstory trees. Thus, acceptable stocking in UEA pine stands has both lower and upper limits, which meet the combined objectives of obtaining acceptable growth rates of merchantable trees and acceptable stocking and developmental rates of reproduction (Table 1). The lower limit is reached when there is a loss in merchantable growth due to under-

Table 1
Acceptable stocking levels in uneven-aged loblolly-shortleaf pine stands (Adapted from Baker et al. (1996))

Measurement[a]	Limit	
	Lower	Upper
Merchantable basal area (m^2/ha)	10	17
Sawtimber basal area (% of merchantable)	60	80
Merchantable volume (m^3/ha)	70	140
Sawtimber volume (m^3/ha)	35	105

[a] Merchantable trees are >9 cm DBH; sawtimber trees are >24 cm DBH. Volumes are inside bark.

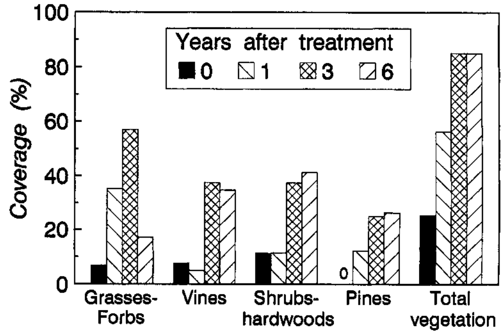

Fig. 1. Coverage of understory vegetation following the initial harvest and competition control implementing uneven-aged silviculture in a pine-hardwood stand in southwestern Mississippi with a site index of 28 m at 50 years. Overstory basal area was 14 m^2/ha in shortleaf and loblolly pines after harvest. Competition control was: harvest of all hardwoods >14 cm DBH, stem-injected herbicide for hardwoods 1.5 to 14 cm DBH, and foliar-applied herbicide to sprouting hardwoods during the first growing season after harvest. (Adapted from Shelton and Murphy (1993) and unpublished data on file at the Southern Research Station, Monticello, AR 71656-3516).

stocking, and the upper limit occurs when merchantable trees adversely affect pine regeneration.

Cutting cycles are based on the residual basal areas, growth rates, operability limits for harvests, and landowner objectives. Cutting cycles typically range from 3 to 10 years on good sites (site index of >26 m at 50 years) and from 8 to 20 years on poor sites (site index <20 m) (Baker et al., 1996). The lower limit for cutting-cycle length is set by the minimum operable cut, while the upper limit occurs when stocking exceeds recommended levels. For stand regeneration, there may be some advantages to cutting cycles of moderate length, e.g., 5 years on good sites and 10 years on poor sites. These cutting cycles are short enough to provide multiple opportunities for regeneration, and they provide a compromise between the positive effects of logging for seedbed preparation and the negative effects associated with potential damage to existing regeneration.

2.2. Understory vegetation

2.2.1. Successional trends

Natural plant succession exerts a dominant influence on stand development in the southeastern United States. Despite intensive efforts to establish and maintain pure pine stands, they are quickly invaded by a succession of competing species. The soils and climate of the southeastern United States favor the development of a predominately hardwood forest, and with the exclusion of periodic disturbance, such as wildfire or management, a stand dominated by the shade-intolerant pines will eventually be replaced by more shade-tolerant hardwoods (Switzer et al., 1979; Cain and Shelton, 1996b).

At best, the most intensive levels of competition control will only temporarily arrest successional changes in UEA pine stands (Cain and Yaussy, 1984). After harvesting and competition control, a new cycle of successional changes begins in the understory of UEA pine stands (Fig. 1). There is a rapid bloom of herbaceous vegetation that dominates the understory during the first year after treatment and then peaks at 3 years with nearly 60% horizontal coverage. Coverage of vines, mainly *Rubus* spp., increases rapidly after the first year but are still a substantial component of the understory at 6 years. Coverage of nonpine woody vegetation and pines also increases rapidly from 1 to 3 years, and then stabilizes at levels of about 40% for nonpine-woody vegetation and 25% for pines. Successional changes after 6 years are characterized by the pines growing above understory hardwoods, and vines and herbaceous vegetation being reduced by shading from both pines and hardwoods. Successional trends in the understory depend on site quality, pine seed crops, and the type of competition control used at the time of the reproduction cut.

A recurring hardwood component develops between competition control treatments applied in UEA pine stands on the Crossett Experimental Forest in southeastern Arkansas, reaching up to 35,000 rootstocks/ha 7 years after control (Cain, 1994a). In dry years, these hardwoods may reduce the radial increment of pines by 30% to 40% (Grano, 1970b). However, the most critical influence of competing vegetation in UEA stands is expressed in suppressing establishment and development of pine regeneration rather than reduced growth rates in merchantable trees (Wahlenberg, 1960; Schultz, 1997).

Without some type of vegetation management, the application of UEA silviculture to shade-intolerant species, such as loblolly and shortleaf pines, will cause a shift in species composition to the shade-tolerant ones. This change in composition is typically a major limitation in the application of UEA silviculture to intolerant species (Chapman, 1942; Franklin, 1976). In the southern pines, successful application of UEA silviculture has always been associated with aggressive competition control (Reynolds, 1959). Herbicides are the principal means of hardwood control, because periodic fire and mechanical treatments may destroy pine regeneration along with competing vegetation.

Rates of plant succession and the associated levels of competing nonpine vegetation are highly correlated with site quality in the southeastern United States. Successional changes are more rapid and intense on good pine sites than on poor sites. Forest managers can use this relationship to gauge how difficult it will be to achieve regeneration in UEA pine stands. In a regional study, for example, Shelton and Murphy (1994) found that increasing site index was negatively correlated with stocking of pine seedlings and saplings in UEA loblolly pine stands. The reason for this paradox – that the best sites for pine growth are the worst sites to regenerate naturally – is clear when levels of competing vegetation are shown (Fig. 2). Site index was positively correlated with the ground coverage of some types of competing vegetation. Site index reflects the availability of limited resources, especially water and nutrients. On the better sites, competing vegetation is often able to respond more quickly than pine regeneration and usurp the resource-rich environment created by harvesting and competition control. Wenger and Trousdell (1958) observed that the success of pine release was greater on the drier sites because of the lower vigor and density of hardwood sprouts. Even on poor sites, Murphy et al. (1991) observed that regenerating UEA shortleaf pine stands in the Ouachita Mountains may be more difficult to obtain on north facing slopes because of more intense competition. The positive relationship between site quality and the intensity of competing vegetation is well known throughout the range of loblolly and shortleaf pines (Coile, 1950; Brender and Davis, 1959; Schuster, 1967; Reed and Noble, 1986). In addition to suppressing regeneration, the dense understory vegetation in UEA pine stands occurring on good sites reduces visibility and makes walking and working difficult.

2.2.2. Control methods

Uneven-aged pine silviculture can be applied on most upland sites in the southeastern United States, but sites characterized by a high percentage of ground cover from herbaceous and nonpine woody competition will require a firm, long-term commitment to vegetation management from the landowner to achieve success. Even-aged silvicultural techniques

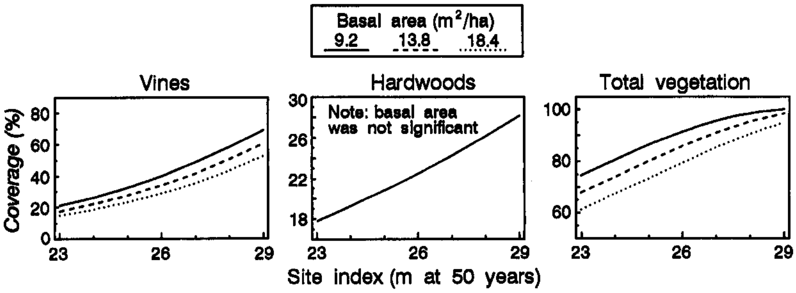

Fig. 2. Coverage of vines, hardwoods, and total understory vegetation 5 years after harvesting and competition control in uneven-aged loblolly pine stands in northern Louisiana and southern Arkansas. Coverage of grasses, forbs, and shrubs was not significantly affected by either site index or basal area and averaged 19%, 5%, and 10%, respectively. (Adapted from Shelton and Murphy (1994)).

Table 2
Typical condition of competing vegetation in uneven-aged pine stands and some control alternatives (Adapted from Baker et al., 1996)

Competing vegetation	Control alternative
Excessive overstory or midstory hardwoods (basal area >2.3 m^2/ha in trees >9 cm DBH).	Cut and sell if operable, or cut and leave, or inject with herbicide.
Dense understory hardwoods with fewer than 500 free-to-grow pine seedlings/saplings per ha.	Release individual pines by mechanical or herbicide removal of overtopping hardwoods, or apply broadcast herbicide treatments.
Herbaceous vegetation and/or vines that prevent development of pine seedlings and saplings.	Apply a broadcast treatment with approved, selective herbicide.
Excessive hardwood basal area (>2.3 m^2/ha) or vines in even-aged stands that are to be converted to uneven-aged structure.	Conduct at least three annual or biennial prescribed, winter burns before the first basal area-reduction harvest, and cut residual hardwoods or inject with herbicide.

may be better suited in these situations because successful pine regeneration must be met only once in an even-aged rotation, rather than periodically as required in UEA stands. Application of UEA silviculture is often very difficult where exotic plants severely limit the success of pine regeneration, because control techniques can be expensive and may require multiple applications. Heavy concentrations of exotic vines, such as kudzu (*Pueraria lobata* [Willd.] Ohwi) and Japanese honeysuckle (*Lonicera japonica* Thunberg), can be particularly troublesome to establishment of pine regeneration.

There is no single competition control method that is suited for all stand conditions and sites, and prescriptions must be developed for each UEA stand (Table 2). In most situations, broadcast applications of selective herbicides will effectively control competing vegetation without destroying pine regeneration in UEA stands managed by single-tree selection (Cain, 1993a).

Alternative vegetation management techniques have generally proven less effective than herbicides. Mechanical treatments, such as mowing and light disking, have been tested for site preparing small openings that have failed to regenerate with pines in UEA stands (Cain, 1987). As small seedling and sapling pines cannot be seen in dense thickets of vines, hardwood brush, and brambles, mowing destroys most of the established pines along with the competing vegetation. Moreover, light disking after mowing is generally not effective in destroying woody nonpine root systems, which sprout prolifically. Concomitantly, chain-saw felling of hardwoods without herbicide application to the stumps tends to result in multiple sprouts with excessive ground cover that can shade out pine seedlings within 1 year after hardwood control and pine establishment (Cain, 1993b)

Investment in competition control can be substantial in managing UEA pine stands, especially on good sites, but frequent revenues generated by cycle cuts help defray this cost. In addition, revenues are fairly high because most of the harvested volume consists of high-quality sawlogs (Baker et al., 1996). Competition control applied periodically in UEA pine stands has multiple benefits – it promotes high rates of timber growth, releases overtopped pine regeneration, and site prepares unoccupied areas for establishment of new seedlings.

Applying competition control in stands regenerated using group selection requires a different approach than single-tree selection. Competition control is applied every time that group openings are created, which normally occurs during each cutting cycle, and can be restricted to these newly created openings. In our experience, low-intensity competition control can be used when the harvested pine timber volumes are high and when merchantable hardwoods (>14 cm DBH) can be sold and harvested (Shelton, 1998). For some landowners, retention of a hardwood component between openings may be desirable to enhance nontimber resources. Cain (1991b) showed that mid-canopy hardwoods suppress the development of understory herbaceous vegetation, which facilitates pine establishment after reproduction cutting and hardwood control.

Prescribed burning is generally not an option in UEA management because fire destroys the pine regeneration required to sustain UEA stands (Crow and Shilling, 1980). Some exceptions to this rule might include stands with very long cutting cycles, group selection, or stands with no existing regeneration in size classes susceptible to fire. In UEA stands lacking regeneration or in even-aged stands being converted, prescribed burning may be used as a remedial treatment for both competition control and seedbed preparation (Table 2).

Use of irregular burning cycles may facilitate pine regeneration in UEA stands (Cain, 1994b). In this technique, stands are subjected to a series of annual or biennial prescribed winter burns until an adequate seed crop occurs; then burning is suspended until most of the regeneration reaches a fire-tolerant size class (>3.8 cm in groundline diameter or >2.4 m tall). When considering a prescribed burning program in UEA pine stands, more attention should be given to density, quadrat stocking, and size of established pine regeneration and to pine seed crops rather than adhering to a rigid burning schedule (Cain, 1993c).

Shortleaf pine regeneration may be more silviculturally suited to the use of prescribed fire in UEA stands than loblolly pine. Most shortleaf pine seedlings develop a sharp J-shaped crook at the ground line which seems to be an adaptation to fire (Walker and Wiant, 1966). Associated with this crook are dormant buds that are protected by the lower portion of the forest floor and soil surface. These buds have a much better chance of surviving a fire than the above-ground portion of stems. Mattoon (1915) contended that most of the virgin pine stands in the Ouachita Mountains, which have the highest concentration of pure stands of this species, developed from sprouts probably associated with fires.

2.3. Seed production

Forest managers can affect seed production within a stand by promoting the vigor, quality, and density of residual trees. This is routinely done during regulation of UEA stand structure, where a component of high-quality trees of seed-producing sizes is always retained within the stand. Intensively managed UEA stands tend to exhibit high levels of pine seed production (Stephenson, 1963). Grano (1970a) found greatest seed production at basal areas of 14 to 16 m^2/ha in loblolly and shortleaf pine stands with a long history of UEA silviculture. Shelton and Murphy (1994) reported that stocking of pine seedlings was positively correlated with maximum diameter and basal area in UEA loblolly pine stands. They attributed these relationships mainly to increased seed production. It seems logical that stand structure would affect levels of seed production due to its influence on the size-class distribution of trees in the residual stand.

The effect of tree size on seed production is well established for both loblolly and shortleaf pines (Mattoon, 1915; Barrett, 1940). Recommendations for natural regeneration methods call for retaining seed trees ≥30 cm DBH because of their higher potential for seed production (Grano, 1957; Lawson, 1986). Increases in maximum diameter increase the percentage of stand basal area in trees of high seed production, while increasing the q factor decreases this percentage (Fig. 3). Due to this relationship, we recommend adopting maximum diameters ≥40 cm in stands with a q factor of 1.2, which provide at least one-third of stand basal area in trees of high seed-production potential.

Inherent variation in annual pine seed crops exceeds the ability of managers to control seed production, and dominant influences are weather, pathogens, and seed and cone predators (McLemore, 1977). In loblolly and shortleaf pines, more than 2 years are needed between flower initiation and seed maturity. During that time,

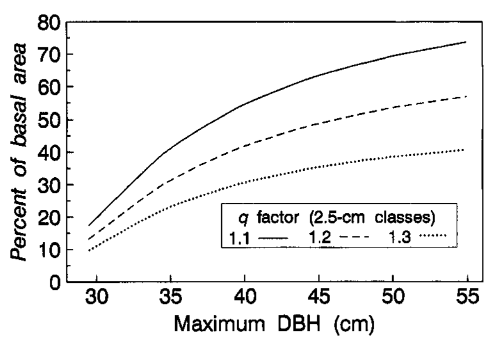

Fig. 3. Maximum DBH and q factor, which are varied to control uneven-aged stand structure, affect the percentage of stand basal area in trees of high seed-producing potential (≥30 cm DBH).

at least five chemical and physiological mechanisms contribute to the pine reproductive cycle: hormones, nutrients, soil moisture, light, and temperature (Barnett and Haugen, 1995). Loblolly pine is classified as a moderate seed producer, while shortleaf pine is generally considered less productive than loblolly pine (Barnett and Haugen, 1995). Annual seed crops are highly variable, fluctuating from near zero to several million per ha with no predictable pattern (Cain and Shelton, 1996a; Shelton and Wittwer, 1996; Wittwer and Shelton, 1992). Seed-crop failures occur about once in 5 years in loblolly pine stands on the West Gulf Coastal Plain (Campbell, 1967; Grano, 1973; Cain and Shelton, 1996a). Seedbeds generally remain receptive for 2 years on good sites and perhaps longer on poor sites. Thus, the probability of successful regeneration in this region is good. Poor seed crops (<100,000 sound seeds/ha) are more common for loblolly pine in the Piedmont (Brender and McNab, 1972) and for shortleaf pine throughout its range (Wittwer and Shelton, 1992).

Throughout the southeastern United States, the frequency of good seed crops is 3 to 6 years for both loblolly (Baker and Langdon, 1990) and shortleaf (Lawson, 1990) pines. However, at the Crossett Experimental Forest in southeastern Arkansas, good or better seed crops (>100,000 sound seeds/ha) were produced in 3 out of 4 years over a 16 year period (Fig. 4). Bumper seed crops with >2,000,000 sound seeds/ha occurred 25% of the time and poor seed crops occurred 25% of the time. Back-to-back seed-crop failures were never recorded.

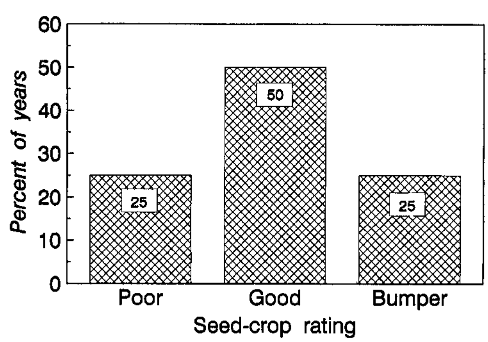

Fig. 4. Qualitative ratings for loblolly and shortleaf pine seed crops during 16 years of monitoring at the Crossett Experimental Forest in southeastern Arkansas. Classes are: poor < 100,000 sound seeds/ha, good = 100,000 to 2,000,000 sound seeds/ha, and bumper > 2,000,000 sound seeds/ha. (Adapted from Cain and Shelton (1996a)).

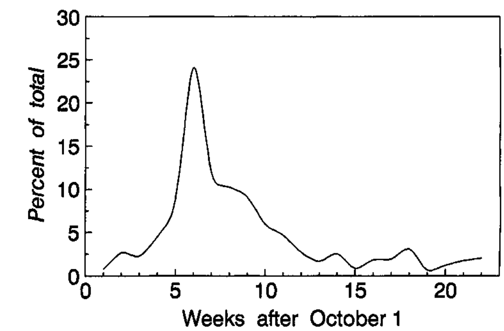

Fig. 5. Average weekly dispersal of loblolly and shortleaf pine seeds during eight good seed crops at the Crossett Experimental Forest in southeastern Arkansas. (Adapted from Cain and Shelton (1996a)).

On poor sites in the Ouachita and Ozark Mountains, where pure stands of natural shortleaf pine are common, seed crops are more episodic (Shelton and Wittwer, 1996). Over a 9 year period, annual seed production averaged about 250,000 sound seeds/ha. Good seed crops were produced about every other year except in the western portion of shortleaf pine's range, where periods of up to 6 years occurred without good seed crops.

On the Crossett Experimental Forest, seed dispersal began in late October and peaked during early November (Fig. 5). An 8 year evaluation of loblolly pine seed production and dispersal in North Carolina showed similar trends (Jemison and Korstian, 1944). In southeastern Arkansas, Grano (1971) found loblolly-shortleaf pine seedfall to be 77% complete by the end of November and 92% by the end of December. Compiling the data from four different sources for shortleaf pine, Wittwer and Shelton (1992) reported that seed dispersal began in late October and was about 70% complete by the end of November and 90% by the end of December.

The winged seeds of loblolly and shortleaf pines are wind disseminated. Although most seeds are dispersed near the parent tree, distribution of loblolly and shortleaf pine seeds probably does not adversely affect the spatial arrangement of regeneration in UEA stands, because dispersal distances are relatively short.

Virtually all residual loblolly and shortleaf pine seeds that remain viable through the winter following dispersal germinate in the spring. Under normal conditions, there is little carryover of viable seeds in the forest floor from one year to the next (Little and Somes, 1959; Barnett and McGilvray, 1991). However, Cain and Shelton (1997) showed that some loblolly seeds may be retained in the old cones of live trees or the tops of trees harvested after cone maturity, although this phenomenon probably contributes little to natural regeneration.

The minimum seed supply needed for successful regeneration depends on stand and site conditions. If other factors are favorable, we feel that 100,000 to 225,000 sound seeds/ha are needed for successful natural regeneration of loblolly and shortleaf pines in UEA stands. In UEA stands dominated by shortleaf pine, Shelton and Murphy (1993, 1997) reported that seedling-to-seed percentages typically range from 1% to 2%. Seedling-to-seed percentages are somewhat higher in stands dominated by loblolly pine, where values are in the vicinity of 5% (Cain, 1991a).

2.4. Seedbed conditions

Each plant species has particular seedbed requirements, and a basic tenet of natural regeneration is to favor the targeted species by creating favorable seedbed conditions (Smith, 1986). Being wind disseminated, loblolly and shortleaf pine seeds are deposited on top of the forest floor, and thus, the covering of the soil surface is the seedbed. In some cases, seed movement after dispersal may be associated with surface water flow or logging activity. The typical seedbed in an undisturbed stand is a forest floor consisting of unincorporated litter of variable thickness. However, skidding and logging traffic during the cycle cuts in UEA stands scrapes away litter from some areas, exposing or perhaps displacing mineral soil. Elsewhere within the stand, litter is disturbed but not completely removed, or litter may be enhanced through piling or deposition of logging debris.

Germinating pine seeds and young seedlings live their first few critical weeks in small microsites only a few centimeters in any dimension. Seedbed conditions affect the microsite's environment as pine seeds overwinter and then germinate during spring, and as the young seedlings become established. Environmental conditions that control germination and early seedling development differ from those that are important after the tops and roots have extended a few centimeters above and below the soil surface. For example, environmental conditions beneath a dense canopy may be favorable to a germinating seed, but these effects become detrimental as the seedling's requirements for both light and moisture increase.

The inhibitory effects of forest floor litter on the germination and establishment of small, wind-disseminated seeds are well known for loblolly and shortleaf pines (Cain, 1991a; Shelton, 1995a, b). Pine seeds have a greater chance for successful germination and establishment when in contact with mineral soil than with litter. Following a bumper seed year, Grano (1949) found a negative exponential relationship between litter depth and pine seedling establishment in loblolly-shortleaf pine stands in southeastern Arkansas (Fig. 6). Although the number of seedlings sharply declines with litter depth, there is no point at which establishment is totally prevented. The occurrence of seedling establishment even at the deepest litter levels undoubtedly reflects the highly variable nature of the forest floor. A few suitable microsites can apparently exist within a generally unfavorable seedbed.

Under controlled conditions, Pomeroy (1949) found that germination of loblolly pine seeds depended on their capacity to absorb moisture from the substrate. Seeds in contact with moist soil were observed to germinate rapidly, while germination of seeds in contact with decomposing litter was restricted. Most seedling mortality (83%) resulted from failure of the radicle to come in contact with a substrate that could

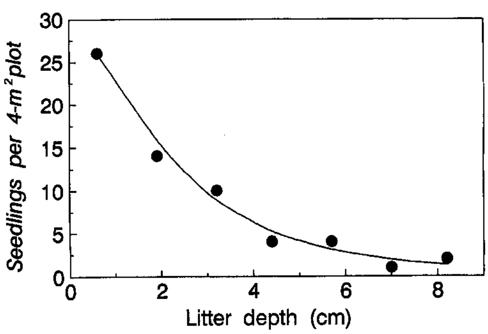

Fig. 6. Relationship between litter depth and establishment of pine seedlings after a bumper crop in uneven-aged loblolly-shortleaf pine stands in the Crossett Experimental Forest in southeastern Arkansas. (Adapted from Grano (1949)).

be penetrated. The second most prevalent cause of seedling mortality (11%) observed by Pomeroy was damping-off, which is also associated with high organic matter levels. Seedbed conditions affect germination and early establishment through biology (pathogens, predators), chemistry (pH, nutrients), environment (moisture, light, temperature), and physical structure (depth, composition) (Shelton, 1995b). Seedbed effects may also be modified by weather conditions occurring during germination (i.e., wet versus dry weather and late freezes).

The periodic harvests in UEA stands strongly affect seedbed conditions, but disturbance levels are typically much less than those associated with even-aged reproduction cutting because lower timber volumes are harvested (Shelton and Wittwer, 1992). Seedbed conditions after logging in UEA stands are very heterogeneous and range from exposed mineral soil to deep accumulations of forest floor material and logging debris. The seedbed conditions existing after a typical cycle cut in two 16 ha UEA loblolly-shortleaf pine stands in southeastern Arkansas are shown in Table 3. Undisturbed litter was the most widespread seedbed condition (about 40% of the area) and very little mineral soil was exposed by logging (4% to 6%). The effects of logging on seedbed conditions depend on: (1) site properties, such as soils, terrain, and access; (2) stand conditions, such as harvested volume, tree size, species, and merchantability limits; (3) season and weather conditions; and (4) equipment. Some of these factors, such as termination of logging in wet weather, setting merchantability limits, and controlling access, should be specified in timber-sale contracts.

Table 3
Seedbed conditions after a 5 year cycle cut of two 16 ha demonstration areas with a 50 year history of uneven-aged silviculture on the Crossett Experimental Forest in southeastern Arkansas

Seedbed condition[a]	Stand 1	Stand 2
	Percent of area	
Undisturbed litter	39	38
Disturbed litter	31	31
Logging slash	25	24
Mineral soil	4	6
Natural feature	1	<1

[a] Unpublished data on file at the Southern Research Station, Monticello, AR 71656-3516. Seedbed conditions were evaluated on one hundred 6 m line-transects systematically located in each area. Natural features were mainly coarse woody debris not associated with logging. Harvested timber volume was 49 m^3/ha, and delimbed trees were skidded tree-length with rubber-tired skidders.

Logging slash is probably the poorest seedbed condition for pine establishment. Grano (1949) reported that pine seedling establishment under slash was only one-tenth of that occurring on a seedbed of pine litter. Slash inhibits regeneration by preventing the seeds from reaching mineral soil, producing shade, and providing cover for seed predators. On the other hand, slash has a beneficial effect on soil properties by providing a source of organic matter, holding the forest floor in place, and reducing soil erosion. Regardless of its effects, slash is a necessary by-product of logging, and its mitigation (e.g., slash-reduction burning or disking) is complicated in UEA stands because of the need to protect residual trees and pine regeneration.

Specific guidelines for evaluating the suitability of seedbed conditions are generally lacking for UEA stands. We feel that logging will normally create sufficient areas with exposed mineral soil and disturbed litter to regenerate an area, especially if the seed supply is good and competing vegetation is controlled. From a regeneration standpoint, the areal extent of each condition and its spatial distribution are the critical features of the seedbed that will govern the need for supplemental treatment.

Studies consistently show that more pine seedlings become established on a mineral soil surface, but that is not necessarily the most desirable seedbed condition for stand regeneration. Regeneration goals should be viewed within the context of acceptable limits, site protection, and the relationship between seedbed conditions and competing vegetation. Many studies have noted the dramatic increase in herbaceous vegetation following reproduction cutting, which has principally been attributed to increases in light and moisture. However, seedbed conditions after harvest can also strongly influence the germination and development of a wide assortment of herbaceous species, whose seeds are either dispersed onto the site or stored in the soil (Shelton, 1995b; Yeiser and Rhodenbaugh, 1995). Clearly, loblolly and shortleaf pines and many of their competitors have similar seedbed requirements. Thus, when the pine seed supply is adequate, a litter seedbed may actually be favorable to natural pine regeneration because it suppresses the development of herbaceous vegetation and may reduce problems with pine overstocking.

3. Factor interactions and timing

The previously discussed factors affecting regeneration do not function independently, but they interact collectively to determine the density of regeneration in UEA stands and its spatial distribution. Some of these factors, such as overstory basal area and understory competition, can be manipulated by management. However, most forest managers can schedule competition control more easily than harvesting because operational timber-sale contracts may extend over several years and stumpage prices may vary seasonally. Although managers can enhance seed production to some degree, inherent variation due to uncontrollable fluctuations in weather and in seed and cone predators set the overall pattern. Each of these controlling factors also has a unique range of suitable limits. Overstory basal area in managed UEA pine stands is rarely allowed to exceed the upper threshold of acceptability (i.e., 17 m^2/ha) to the point that a regeneration failure occurs, and seedbed conditions will not normally be so unfavorable that they prevent regeneration establishment. By contrast, seed production and nonpine competing vegetation can be so unfavorable that regeneration failures occur. These intricate and variable relationships emphasize the importance of timing and risk that complicate the establishment of regeneration in UEA stands and challenge forest managers.

We feel that although all factors are important, the timing between low levels of competing vegetation and a good seed crop is the most important key to regeneration success in UEA pine stands. The window of opportunity to secure regeneration after competition control depends on the initial stand conditions, site quality, and type of competition control implemented (Trousdell, 1954; Grano, 1971). On most good Coastal Plain sites, acceptable conditions generally exist for about 2 years after competition control, while 3 to 5 years may be more typical for poor sites in the Ouachita Mountains. When harvesting and competition control are conducted together, the seed crop occurring during the year of stand treatment will have a pronounced effect on the resulting regeneration (Cain, 1991a; Shelton and Murphy, 1994). When a pine seed falls on a 1-year-old seedbed, where fresh litter covers the mineral soil exposed by logging and where competing vegetation has a 1 year growth advantage, that seed has a lower probability of germinating and developing into a well-established seedling. The loss of favorable conditions results in a progressive decline in the seedling-to-seed percentage, but this can be partially offset by a good seed crop.

Based on these relationships, there are probably two silviculturally sound approaches to regenerating UEA stands. The first can be applied in regions with fairly good and consistent seed crops by managers familiar with natural regeneration. Regeneration levels can be periodically inventoried, and when found to be deficient due to competing vegetation, competition control can be applied before an upcoming cycle cut. The probability that an acceptable seed crop will occur after harvesting and competition control is fairly good. Under these circumstances, more intensive competition control techniques, such as broadcast application of herbicides, may be needed to extend the window-of-opportunity for natural regeneration as long as possible; this is especially true on good sites that are rapidly occupied by herbaceous vegetation and vines after harvest. Reynolds (1959) successfully managed UEA pine stands on the Crossett Experimental Forest in southeastern Arkansas using this approach. In addition, Reynolds did not worry when a given cutting cycle failed to yield pine regeneration, because the cutting cycles were short, pine seed crops were usually good, and competing nonpine vegetation was periodically controlled. Reynold's general rule-of-thumb was that substantial regeneration should be established at least every other cutting cycle.

The second approach is more suitable where low or erratic natural pine seed production limits regeneration success. Foresters can time competition control, which is comparatively easy to schedule, when a good seed crop is predicted. Potential seed crops can be assessed some months in advance of dispersal by evaluating flowers or developing cones (Trousdell, 1950; Shelton and Wittwer, 1995). Usually, cone counts or cone-rating systems are employed in forest situations to predict seed production. Cone assessments are made by viewing the crowns of standing trees with binoculars during early morning in the late summer, when the current year's cone crop is most visible. In general, the higher the cone count, the better the potential seed crop. Cone counts can also be made on felled trees in late summer. These forecasting techniques provide only a relative measure of seed production in the absence of actual monitoring, but they may be useful for planning harvests or competition control in advance of seed dispersal. To obtain the maximum number of seedlings from a seed crop, competition control should be completed by late summer or early fall, to coincide with the time of peak seed dispersal, and should be done only when adequate seed crops are predicted. In addition, the intensity of site preparation can often be less when treatment coincides with a bumper seed crop, but intensive site preparation has not been found to be beneficial to establishing pine regeneration when seed crops are poor (Cain, 1991a).

4. Inventory procedures and acceptable stocking levels

Stocking is generally determined separately for the merchantable and submerchantable components of UEA pine stands. The need for evaluating the establishment and development of regeneration depends on stand and site conditions and the experience of the managing forester. Frequent evaluations are not needed in locations where regeneration is easily obtained and develops rapidly, but greater attention must be paid to regeneration in stands lacking good structure in merchantable size classes. Generally, it is best to evaluate regeneration every time the merchantable stand is inventoried, which is usually recommended before every other cutting cycle (Baker et al., 1996).

There is no single acceptable method for inventorying pine regeneration within UEA stands. Some procedures recommend using nested temporary plots to count well-established seedlings (<1.5 cm in DBH) in 4 m^2 circular plots and saplings (1.5 to 9.0 cm DBH) in 40 m^2 circular plots (Farrar, 1996). Counting individual stems can be very time consuming, and density is often a poor measure of regeneration in UEA stands because of its clumped spatial distribution (Shelton and Murphy, 1994). An alternative is to simply record whether a 4 m^2 circular plot is stocked with at least one submerchantable pine (0.3 m tall to 9 cm DBH) (Baker et al., 1996). Information is also collected on whether the dominant submerchantable pine on the plot is free-to-grow or overtopped by competing vegetation. For plots with only overtopped pines, the type of competing vegetation that is overtopping the regeneration (e.g., grass, forb, vine, hardwood, or shrub) should be recorded to aid in developing silvicultural prescriptions for competition control. Whether the 4 m^2 plot is beneath the crown of a merchantable-sized pine or hardwood is also recorded. Reynolds (1959) used 100 regeneration plots (4 m^2) for each 16 ha of stand area, and we feel this is appropriate for most stand conditions.

The stocking of regeneration in UEA pine stands is critical to the sustainability of timber production because regeneration provides ingrowth to merchantable size classes. However, stocking of regeneration in UEA stands is much less critical than in their even-aged counterparts, because of retained merchantable trees and multiple regeneration opportunities provided by UEA silviculture. There is probably no single minimum stocking level for acceptable regeneration in UEA pine stands, because acceptable stocking depends on stand and site conditions, structural goals, and the need for regular and uniform harvests by the landowner. Although specific standards vary, most authorities suggest that a well-stocked UEA pine stand should have at least 250 to 500 submerchantable pines per ha (Reynolds, 1959; Baker et al., 1996; Farrar, 1996). However, Farrar adds that two to three times this number would provide a built-in safety factor, accounting for losses due to competition, logging, and other stand disturbances. For inventories using 4 m^2 plots, submerchantable stocking should range from a minimum of 20% to an optimum of 50% in UEA pine stands (Reynolds, 1959; Baker et al., 1996). Ideally, these stocking levels should exist after logging disturbance. Most of the concern about stocking thresholds in UEA pine stands is in regard to minimum levels rather than maximum, and in most stand conditions, overstocking in submerchantable size classes is not considered to be a problem (Cain et al., 1987).

Another indication of the general health and vigor of pine regeneration is that most stems should be growing at least 0.2 m/year in height; annual height growth is apparent from the flushing pattern of loblolly and shortleaf pines. Pines exceeding this threshold have a high probability of survival and will respond if released (Chapman, 1942; Wahlenberg, 1960). Cain et al. (1987) also suggested that the dominant submerchantable pines in UEA stands should have a live-crown ratio of ≥40%.

Reynolds (1959) offers an approach for expressing the combined stocking of both the merchantable and submerchantable component of UEA pine stands. He determined the percentage of 4 m^2 inventory plots with a submerchantable pine and/or plots beneath the crown of a merchantable pine in twenty-four 16 ha UEA stands. An average of 53% of the plots were stocked with a submerchantable pine and 47% with a merchantable pine. When both merchantable and understory pines were considered, 81% of the plots were stocked by pines, which Reynolds considered to be good stocking for UEA pine stands.

5. Protection

The multiple size and age classes present in UEA stands provide some level of protection against damaging agents. Windthrow, ice breakage, insects, diseases, and fire may adversely affect some of the size classes, but rarely is the entire stand devastated. In our experience, pathogens and insects usually do not adversely affect the regeneration in UEA pine stands, and other than competition, the most destructive agents are drought, fire, and logging damage.

Periodic droughts occasionally cause extensive and severe mortality of first-year seedlings. Reynolds (1959) noted that the 1935 and 1951 seed crops were excellent at the Crossett Experimental Forest in southeastern Arkansas, but were followed by severe droughts that killed many seedlings. Trousdell and Wenger (1963) found that April to June rainfall was particularly critical in the establishment of first-year seedlings. Droughts occurring during the latter part of the growing season rarely result in complete mortality of new seedlings. For example, Shelton and Murphy (1997) observed that a drought occurring from June to August of 1990 resulted in 40% mortality of first-year shortleaf pine seedlings on a poor site in the Ouachita Mountains where the merchantable pine basal area was 14 m^2/ha. The mortality rate doubled to 80% when a hardwood basal area of 7 m^2/ha was retained along with the pines, indicating that competition control may be a way to reduce the risks of drought mortality.

Protection from wildfire is critical in UEA stands because of the presence of multiple size classes. Seedlings less than 1.5 m tall are particularly vulnerable to fire (Wahlenberg, 1960). Fuel loads are fairly high because of dense understory vegetation and the litter produced by merchantable trees. The risks of wildfire are particularly high when broadcast herbicides are applied in late summer and browning occurs before onset of the normally wet winters. Should a wildfire occur in an UEA stand, a cohort of new regeneration will normally rapidly replace killed seedlings because of the resulting seedbed preparation and competition control. An advantage of shortleaf pine is that top-killed seedlings and saplings may sprout.

Perhaps the greatest risk to regeneration in UEA pine stands is damage incurred during logging; these risks also apply to retained merchantable trees. Some damage to regeneration is going to occur even in the most favorable conditions; thus, a realistic goal for the forest manager is to keep damage within acceptable limits. Particular care is needed in stands lacking good structure in merchantable size classes but with a cohort of developing regeneration, which will be critical in developing a well-structured stand in the future. Less attention is needed in stands without regeneration or in stands with good structure in merchantable size classes. In many cases, regeneration may be excessive and logging damage provides a degree of precommercial thinning. Damage occurs from multiple sources during a logging operation: to gain access to harvested trees, in felling, cutting branches and tops, and skidding logs. Wahlenberg (1960) commented on the flexibility of young pines that are ≤1.5 m tall and stated that many can be knocked down during logging and recover.

Logging damage to regeneration is a subject that has not been adequately researched, but there are some common-sense practices to follow. Careful planning is needed to establish skid trails and log decks. Damage will be less if trees are felled in the direction that they will be skidded, especially if skid trails are straight. Mid-sized skidding equipment is well suited to harvesting the moderate timber volumes provided by cycle cuts in UEA stands and will minimize damage to both regeneration and residual trees. Branches and tops must be cut from felled trees before logs are skidded. Skidding shorter log lengths (e.g., 10 m logs) will reduce damage to both regeneration and residual trees, but tree-length skidding is also possible if carefully done. We have found that the larger maximum diameters result in less logging disturbance because fewer trees have to be cut and skidded to obtain the allowable cut (unpublished data on file at the Southern Research Station, Monticello, AR 71656-3516). In addition, Shelton and Murphy [in press] reported that logging disturbance in UEA stands is positively correlated with the harvested timber volumes.

Special care is required when logging poorly drained sites on the Coastal Plain during the winter and spring because of saturated soils. Managers should carefully monitor such operations and be ready to terminate activities should excessive rutting and soil damage occur. Steep slopes in the Ouachita Mountains, ranging up to 50%, also complicate logging. Wahlenberg (1960) stated that skidding along a contour in hilly terrain causes the logs to roll, which may damage nearby seedlings. He recommended skidding logs across contours of short slopes, so long as repeat traffic does not promote erosion. It is tempting for loggers to fell trees into openings in UEA stands to reduce damage to merchantable trees, but these openings are where regeneration is most critical. So loggers who are not experienced in harvesting UEA stands must be informed of these special needs, and their activities should be closely monitored. If possible, managers should use contractors with experience in logging partially cut stands. Group selection has some advantages over single-tree selection regarding potential logging damage to regeneration, because the distinctive openings are easily seen and recognized (Murphy et al., 1993).

Poor visibility is one of the greatest challenges to logging UEA stands, especially on good sites where dense understory vegetation (both pines and other species) occurs. Due to this, loggers must cover considerable area looking for trees marked for harvest or for logs to be skidded, which exacerbates the problem of logging damage. In stands with poor visibility, timber markers should place paint marks as high on the boles as possible and should mark the trees on several sides.

6. Conclusions

The UEA silvicultural system is one of several that can be used to naturally regenerate and manage loblolly and shortleaf pines. Some are more suitable to specific site and stand conditions and may meet landowner objectives better than others. It is our hope that this paper will be useful to forest researchers in identifying gaps in the knowledge about UEA pine silviculture, and will also help forest managers meet the regeneration needs in their UEA pine stands.

Uneven-aged stands of loblolly and shortleaf pines will be far easier to create and sustain on the poorer sites because of less competing vegetation and the ease of securing natural pine regeneration. High levels of competing vegetation are associated with the better sites and lower levels of merchantable stand basal area, which stress the importance of periodic competition control under these conditions. Young even-aged stands of loblolly and shortleaf pines often will overcome excessive competing vegetation by sustaining high rates of height growth. However, the overstory maintained in UEA silviculture suppresses height growth, and this intensifies the need for periodic release of pine regeneration from competing vegetation in UEA stands. Without some type of competition control, applying UEA silviculture to shade-intolerant pines is expected to cause a shift in species composition to more shade-tolerant competitors. This change in composition frequently limits the successful application of UEA silviculture for shade-intolerant species. Based on our experience with pine regeneration, group selection has advantages over single-tree selection in the following situations: (1) when a significant hardwood component is desired in the residual stand, (2) where competing vegetation is excessive or where the use of herbicides is restricted, and (3) where regeneration needs protection from logging damage.

Of all the factors affecting seedling establishment in UEA pine stands, seed production is perhaps under the least degree of silvicultural control. Considering this restriction, foresters relying on natural regeneration in UEA stands need to know the periodicity of seed crops in the stands that they manage. As seed production is fairly reliable for loblolly and shortleaf pines in some regions, less attention needs to be paid to annual variation in seed crops. In regions where low seed production limits pine regeneration, managers should try to coincide harvesting and/or competition control with good seed crops. Timing of an adequate seed supply with a receptive seedbed and low levels of competing vegetation is the greatest challenge in securing abundant pine regeneration in UEA stands. The lack of regeneration present in some stands may be of little immediate concern, especially if the merchantable trees display good UEA structure. The short cutting cycles and frequent competition control used in UEA pine stands allow many opportunities to secure acceptable regeneration from natural seedfall. In addition, the residual stand maintained in UEA silviculture moderates the short-term impacts of regeneration problems. By following these basic and proven silvicultural techniques, forest landowners should be able to secure abundant natural regeneration in their UEA stands and reap the benefits of sustained yields.

Acknowledgements

This paper is an expanded version of a poster presented at the IUFRO Symposium on Uneven-Aged Silviculture, 15–26 September 1997, in Corvallis, OR. The contribution of Paul A. Murphy (deceased) to the initial effort is gratefully acknowledged.

References

Baker, J.B., Langdon, O.G., 1990. *Pinus taeda* L. Loblolly pine. In: Burns, R.M., Honkala, B.H. (Eds.), Silvics of North America, vol. 1. Conifers. USDA For. Serv., Agric. Handb. 654, pp. 497–512.

Baker, J.B., Shelton, M.G., 1998. Rehabilitation of understocked loblolly-shortleaf pine stands II. Development of intermediate and suppressed trees following release in natural stands. South. J. Appl. For. 22, 41–46.

Baker, J.B., Cain, M.D., Guldin, J.M., Murphy, P.A., Shelton, M.G., 1996. Uneven-aged silviculture for the loblolly and shortleaf pine forest types. USDA For. Serv., Gen. Tech. Rep. SO-118, 65 pp.

Barnett, J.P., Haugen, R.O., 1995. Producing seed crops to naturally regenerate the southern pines. USDA For. Serv., Res. Pap. SO-286, 10 pp.

Barnett, J.P., McGilvray, J.M., 1991. Carry-over of loblolly pine seeds on cutover forest sites. Tree Planters' Notes 42(4), 17–18.

Barrett, L.I., 1940. Requirements for restocking cutover loblolly and shortleaf pine stands. So. Lumberman 161(2033), 200–202.

Becton, W.R., 1936. Effects of varying densities of hardwood cover on growth and survival of shortleaf pine reproduction. J. For. 34, 160–164.

Bormann, F.H., 1956. Ecological implications of changes in the photosynthetic response of *Pinus taeda* seedlings during ontogeny. Ecology 37, 70–75.

Brender, E.V., Barber, J.C., 1956. Influence of loblolly pine overwood on advance reproduction. USDA For. Serv. South. For. Exp. Sta., Sta. Pap. 62, 12 pp.

Brender, E.V., Davis, L.S., 1959. Influence of topography on the future composition of lower Piedmont forests. J. For. 57, 33–34.

Brender, E.V., McNab, W.H., 1972. Loblolly pine seed production in the lower Piedmont under various harvesting methods. J. For. 70, 345–349.

Cain, M.D., 1987. Site-preparation techniques for establishing natural pine regeneration on small forest properties. South. J. Appl. For. 11, 41–45.

Cain, M.D., 1991a. Importance of seedyear, seedbed, and overstory for establishment of natural loblolly and shortleaf pine regeneration in southern Arkansas. USDA For. Serv., Res. Pap. SO-26, 10 pp.

Cain, M.D., 1991b. Hardwoods on pine sites: competition or antagonistic symbiosis. For. Ecol. Manage., 44, 147–160.

Cain, M.D., 1993a. Releasing uneven-aged loblolly-shortleaf pine stands with operational application of Arsenal AC. In: Street, J.E. (Ed.), Proceedings of the 46th Annual Meeting Southern Weed Science Society, pp. 356–362.

Cain, M.D., 1993b. First-year response of direct-seeded shortleaf pine and hardwood sprouts to three methods of hardwood control in the Arkansas Ozarks. In: Brissette, J.C. (Ed.), Proceedings of the Seventh Biennial Southern Silvicultural Research Conference. USDA For. Serv., Gen. Tech. Rep. SO-93, pp. 317–326.

Cain, M.D., 1993c. A 10-year evaluation of prescribed winter burns in uneven-aged stands of *Pinus taeda* L. and *P. echinata* Mill.: woody understorey vegetation response. Int. J. Wildland Fire, 3(1), 13–20.

Cain, M.D., 1994a. A 7-year evaluation of preharvest hardwood control for enhancing natural regeneration of loblolly-shortleaf pines in an uneven-aged stand. In: Street, J.E. (Ed.), Proceedings of the 47th Annual Meeting Southern Weed Science Society, pp. 240–246.

Cain, M.D., 1994b. Problems and opportunities associated with prescribed burning in uneven-aged management of loblolly and shortleaf pines. In: Proceedings of the 12th International Conference on Fire and Forest Meteorology. S.A.F. Pub. 94-02, pp. 611–619.

Cain, M.D., Shelton, M.G., 1996a. Considerations for natural regeneration of loblolly and shortleaf pines. The Consultant, 41(3), 20–23.

Cain, M.D., Shelton, M.G., 1996b. The R.R. Reynolds Research Natural Area in southeastern Arkansas: a 56-year case study in pine-hardwood overstory sustainability. J. Sustainable For., 3(4), 59–74.

Cain, M.D., Shelton, M.G., 1997. Loblolly and shortleaf pine seed viability through 21 months of field storage: can carry-over occur between seed crops? Can. J. For. Res. 27, 1901–1904.

Cain, M.D., Yaussy, D.A., 1984. Can hardwoods be eradicated from pine sites? South. J. Appl. For. 8, 7–12.

Cain, M.D., Baker, J.B., Murphy, P.A., 1987. Precommercial thinning of pine regeneration in uneven-aged stands. In: Phillips, D.R. (Ed.), Proceedings of the Fourth Biennial Southern Silvicultural Research Conference. USDA For. Serv., Gen. Tech. Rep. SE-42, pp. 419–424.

Campbell, T.E., 1967. Loblolly-shortleaf pine seedfall in Louisiana. J. For. 65, 894–895.

Chapman, H.H., 1942. Management of loblolly pine in the pine-hardwood regions in Arkansas and Louisiana west of the Mississippi River. Yale Univ. Sch. For. Bull. 49, 150.

Chapman, H.H., 1945. The effect of overhead shade on the survival of loblolly pine seedlings. Ecology 26, 274–282.

Coile, T.S., 1950. Effect of soil on the development of hardwood understories in pine stands of the Piedmont Plateau. Soil Sci. Soc. Am. Proc. 14, 350–352.

Crow, A.B., Shilling, C.L., 1980. Use of prescribed burning to enhance southern pine timber production. South. J. Appl. For. 4(1), 15–19.

Farrar, R.M., Jr., 1996. Fundamentals of uneven-aged management in southern pine. Misc. Pub. 9, Tall Timb. Res. Sta., Tallahassee, FL, 52 pp.

Farrar, R.M., Jr., Boyer, W.D., 1991. Managing longleaf pine under the selection systemCpromises and problems. In: Coleman, S.S., Neary, D.G. (Eds.), Proceedings of the Sixth Biennial Southern Silvicultural Research Conference. USDA For. Serv., Gen. Tech. Rep. SE-70, pp. 357–368.

Ferguson, E.R., 1963. Overstory density key to pine seedling survival and growth in east Texas. J. For. 61, 597–598.

Franklin, J.F., 1976. Effects of uneven-aged management on species composition. In: Uneven-aged silviculture and management in the United States. USDA For. Serv., Gen. Tech. Rep. WO-24, pp. 169–175.

Grano, C.X., 1949. Is litter a barrier to the initial establishment of shortleaf and loblolly pine reproduction? J. For. 47, 544–548.

Grano, C.X., 1957. Indices to potential cone production of loblolly pine. J. For. 55, 890–891.

Grano, C.X., 1970a. Seed yields in loblolly-shortleaf pine selection stands. USDA For. Serv., Res. Note SO-109, 4 pp.

Grano, C.X., 1970b. Small hardwoods reduce growth of pine overstory. USDA For. Serv., Res. Pap. SO-55, 9 pp.

Grano, C.X., 1971. Conditioning loessial soils for natural loblolly and shortleaf pine seeding. USDA For. Serv., Res. Note SO-116, 4 pp.

Grano, C.X., 1973. Loblolly pine fecundity in south Arkansas. USDA For. Serv., Res. Note SO-159, 7 pp.

Guldin, J.M., Baker, J.B., 1998. Uneven-aged silviculture, southern style. J. For. 96(7), 22–26.

Guo, Y., Shelton, M.G., 1998. Canopy light transmittance in natural stands on upland sites in Arkansas. In: Waldrop, T.A. (Ed.), Proceedings of the Ninth Biennial Southern Silvicultural Research Conference. USDA For. Serv., Gen. Tech. Rep. SRS-20, pp. 618–622.

Jackson, L.W.R., 1959. Relation of pine forest overstory opening diameter to growth of pine reproduction. Ecology 40, 478–480.

Jemison, G.M., Korstian, C.F., 1944. Loblolly pine seed production and dispersal. J. For. 42, 734–741.

Lawson, E.R., 1986. Natural regeneration of shortleaf pine. In: Murphy, P.A. (Ed.), Proceedings of a Symposium on the Shortleaf Pine Ecosystem. Univ. Arkansas Coop. Ext. Serv., Monticello, AR, pp. 53–63.

Lawson, E.R., 1990. *Pinus echinata* Mill. Shortleaf pine. In: Burns, R.M., Honkala, B.H. (Eds.), Silvics of North America, vol. 1. Conifers. USDA For. Serv., Agric. Handb. 654, pp. 316–326.

Little, S., Somes, H.A., 1959. Viability of loblolly pine seed stored in the forest floor. J. For. 57, 848–849.

Marquis, D.A., 1976. Application of uneven-aged silviculture on public and private lands. In: Uneven-aged Silviculture and Management in the United States. USDA For. Serv., Gen. Tech. Rep. WO-24, pp. 25–63.

Mattoon, W.R., 1915. Life history of shortleaf pine. USDA Bull. 244, 46.

McLemore, B.F., 1977. Strobili and conelet losses in four species of southern pines. USDA For. Serv., Res. Note SO-226, 5 pp.

Murphy, P.A., Baker, J.B., Lawson, E.R., 1991. Selection management of shortleaf pine in the Ouachita Mountains. South. J. Appl. For. 15, 61–67.

Murphy, P.A., Shelton, M.G., Graney, D.L., 1993. Group selection – problems and possibilities for the more shade-intolerant species. In: Gillespie, A.R., Parker, G.R., Pope, P.E., Rink, G. (Eds.), Proceedings of the Ninth Central Hardwood Conference. USDA For. Serv., Gen. Tech. Rep. NC-161, pp. 229–247.

O'Hara, K.L., 1998. Silviculture for structural diversity: a new look at multiaged systems. J. For. 96(7), 4–10.

Pomeroy, K.B., 1949. The germination and initial establishment of loblolly pine under various surface soil conditions. J. For. 47, 541–543.

Reed, D.P., Noble, R.E., 1986. Understory biomass production in central Louisiana. Proc. Louisiana Acad. Sci. 49, 15–22.

Reynolds, R.R., 1959. Eighteen years of selection management on the Crossett Experimental Forest. USDA For. Serv., Tech. Bull. 1206, 68 pp.

Schultz, R.P., 1997. Loblolly Pine – The Ecology and Culture of Loblolly Pine (*Pinus taeda* L). USDA For. Serv., Agric. Handb. 713, Washington, DC, 493 pp.

Schuster, J.L., 1967. The relation of understory vegetation to cutting treatments and habitat factors in an east Texas pine-hardwood type. Southwest. Nat. 12, 339–364.

Shelton, M.G., 1995a. Effects of seed production, seed conditions, and overstory basal area on the establishment of shortleaf pine seedlings in the Ouachita Mountains. USDA For. Serv., Res. Pap. SO-293, 13 pp.

Shelton, M.G., 1995b. Effects of the weight and composition of litter on emergence and early establishment of loblolly pine seedlings. Can. J. For. Res., 25, 80–486.

Shelton, M.G., 1998. Effects of opening size on pine and hardwood regeneration 3 years after group selection cutting in a pine-hardwood stand in southern Arkansas. In: Waldrop, T.A. (Ed.), Proceedings of the Ninth Biennial Southern Silvicultural Research Conference. USDA For. Serv., Gen. Tech. Rep. SRS-20, pp. 343–348.

Shelton, M.G., Murphy, P.A., 1993. Pine regeneration and understory vegetation 1 year after implementing uneven-aged silviculture in pine-hardwood stands of the silty uplands of Mississippi. In: Brissette, J.C. (Ed.), Proceedings of the Seventh Biennial Southern Silvicultural Research Conference. USDA For. Serv., Gen. Tech. Rep. SO-93, pp. 333–341.

Shelton, M.G., Murphy, P.A., 1994. Loblolly pine regeneration and competing vegetation 5 years after implementing uneven-aged silviculture. Can. J. For. Res. 24, 2448–2458.

Shelton, M.G., Murphy, P.A., 1997. Understory vegetation 3 years after implementing uneven-aged silviculture in a shortleaf pine-hardwood stand in the Ouachita Mountains. USDA For. Serv., Res. Pap. SO-296, 13 pp.

Shelton, M.G., Murphy, P.A., Disturbance from the initial harvest implementing uneven-aged silviculture in a pine-hardwood stand in southwestern Mississippi. In: Haywood, J.D. (Ed.). Proceeding of the Tenth Biennial Southern Silvicultural Research Conference. USDA For. Serv., Gen. Tech. Rep. SRS, in press.

Shelton, M.G., Wittwer, R.F., 1992. Effects of seedbed condition on natural shortleaf pine regeneration. In: Brissette, J.C., Barnett, J.P. (Eds.), Proceedings of the Shortleaf Pine Regeneration Workshop. USDA For. Serv., Gen. Tech. Rep. SO-90, pp. 124–139.

Shelton, M.G., Wittwer, R.F., 1995. Forecasting loblolly and shortleaf pine seed crops. In: Edwards, M.B. (Ed.), Proceedings of the Eighth Biennial Southern Silvicultural Research Conference. USDA For. Serv., Gen. Tech. Rep. SRS-1, pp. 605–612.

Shelton, M.G., Wittwer, R.F., 1996. Seed production in natural shortleaf pine stands in the Ouachita and Ozark Mountains. South. J. Appl. For. 20, 74–80.

Smith, D.M., 1986. The Practice of Silviculture, 8th ed., Wiley, New York, 527 pp.

Stephenson, G.K., 1963. Ten years of shortleaf pine seed crops in Texas. J. For. 61, 270–272.

Switzer, G.L., Shelton, M.G., Nelson, L.E., 1979. Successional development of the forest floor and soil surface on upland sites of the East Gulf Coastal Plain. Ecology 60, 1162–1171.

Trousdell, K.B., 1950. A method of forecasting annual variation in seed crop for loblolly pine. J. For. 48, 345–348.

Trousdell, K.B., 1954. Favorable seedbed conditions for loblolly pine disappear 3 years after logging. J. For. 52, 174–176.

Trousdell, K.B., Wenger, K.F., 1963. Some factors of climate and soil affecting establishment of loblolly pine stands. For. Sci. 9, 130–136.

Wahlenberg, W.G., 1948. Effect of forest shade and openings on loblolly pine seedlings. J. For. 46, 832–834.

Wahlenberg, W.G., 1960. Loblolly Pine. Sch. For., Duke Univ., Durham, NC, 603 pp.

Walker, L.C., Wiant, H.V., Jr., 1966. Silviculture of shortleaf pine. Stephen F. Austin State College, Bull. 9, 60 pp.

Wenger, K.F., Trousdell, K.B., 1958. Natural regeneration of loblolly pine in the South Atlantic Coastal Plain. USDA For. Serv., Southeast. For. Exp. Sta., Production Res. Rep. 13, 78 pp.

Williston, H.L., 1978. Uneven-aged management in the loblolly-shortleaf pine type. South. J. Appl. For. 2(3), 78–82.

Wittwer, R.F., Shelton, M.G., 1992. Seed production in natural shortleaf pine stands. In: Brissette, J.C., Barnett, J.P. (Eds.), Proceedings of the Shortleaf Pine Regeneration Workshop. USDA For. Serv., Gen. Tech. Rep. SO-90, pp. 113–123.

Yeiser, J.L., Rhodenbaugh, E.J., 1995. Pine growth enhanced with litter management during upland hardwood stand conversion: five-year results. Arkansas Agric. Exp. Sta., Bull. 946, 20 pp.